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中国海相早三叠世弓鲛鱼类(软骨鱼类)的首次报道
——华南二叠系–三叠系界线上下鱼类序列研究之一[1)]

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摘要　广西田东县作登下三叠统罗楼组产出弓鲛鱼类:作登弓鲛 *Hybodus zuodengensis* (Yang et al.)、乐氏弓鲛 *H. yohi* (Yang et al.)和田东多尖齿鱼(新种) *Polyacrodus tiandongensis* sp. nov., 其中前二种化石以前曾被作为牙形类报道。这是弓鲛鱼类在中国海相早三叠世的首次报道。另外,本组还产出属种未定的硬骨鱼类化石(Osteichthyes gen. et sp. indet.)。建立了我国海相早三叠世第一个鱼类带化石,作登弓鲛–乐氏弓鲛组合带(*Hybodus zuodengensis*-*H. yohi* AZ);伴生的有 *Neospathodus homeri*-*N. triangularis* 牙形类带化石,该带化石延续的时限为奥伦尼克阶(Olenekian)司帕斯期(Spathian)早期。

关键词　广西,海相,早三叠世,弓鲛鱼类,带化石

中图法分类号　Q915.862

广西田东县作登登高岭剖面是赵金科先生 40～50 年代研究广西西部早三叠世菊石时实测的下三叠统剖面中最完整、研究较为详细的一个,特别值得关注的是,该剖面下三叠统与下伏的上二叠统地层为整合接触。杨守仁等在 80 年代初又实测了该剖面并逐层系统地采集了各门类化石,例如牙形类和菊石等,其中也包括鱼类化石。鱼类化石产自剖面的 8～11 层。伴生的有牙形类 *Neospathodus homeri*-*N. triangularis* 带化石,它们是世界性的种,常常一起出现于整个 Spathian 期早期(曹延岳、王志浩,1993)。本文涉及的部分鱼化石最初被当作牙形类新属种 *Pachycladina zuodengensis*, *Pseudogondolela yohi* 发表(杨守仁等,1984)。由于这些鱼类化石对探讨我国早三叠世鱼类构成,海相与非海相对比和二叠系–三叠系界线上下鱼类序列的演替,以及古生代和中生代之交鱼类的绝灭、复苏等问题甚为重要,所以本文对这些化石进行了研究(图 1,2)。

1　化石记述

软骨鱼纲　Chondrichthyes Huxley, 1880

板鳃亚纲　Elasmobranchii Bonaparte, 1838

1) 国家自然科学基金项目(编号:49872010)、中国科学院古生物学与古人类学科基础研究特别支持费项目(编号:980101)、国家重点基础研究发展规划项目(编号:G2000077705)资助。

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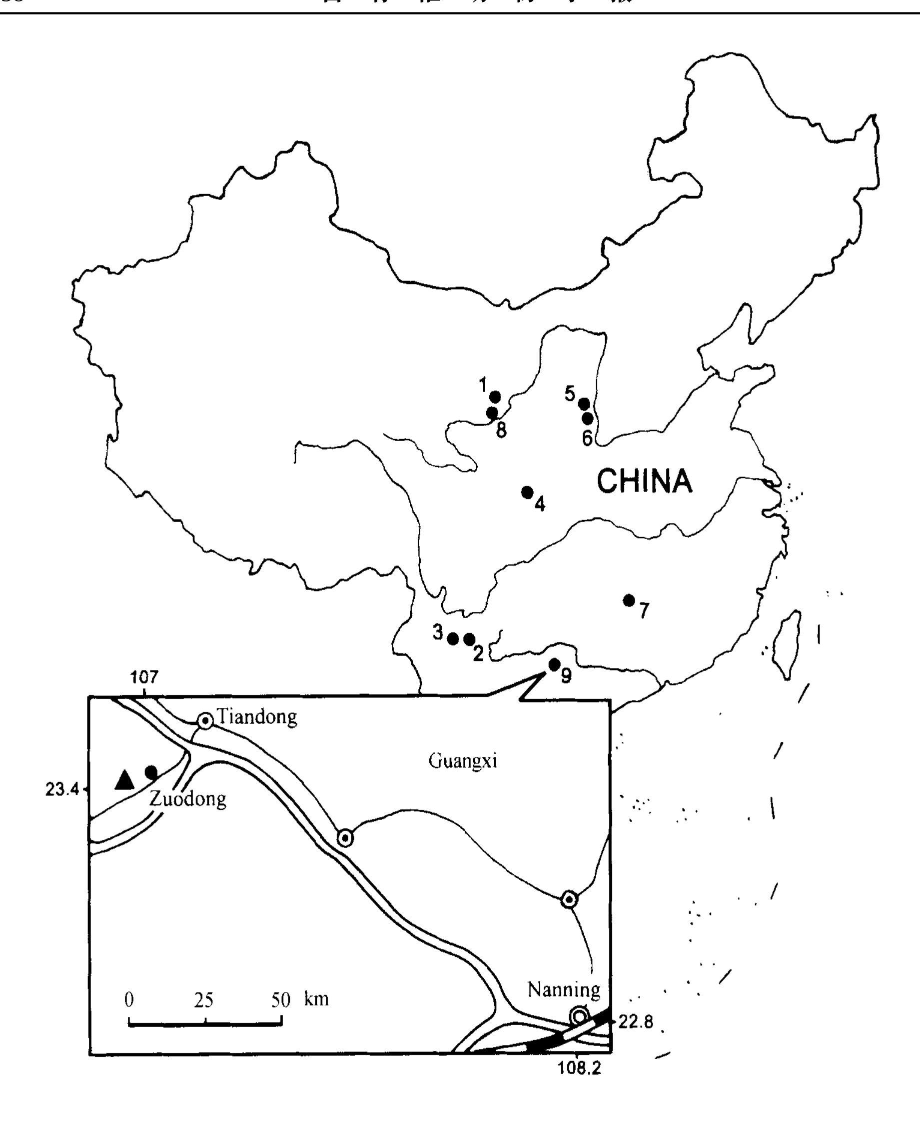


图1　中国弓鲛鱼类化石分布和作登化石产地示意图

Fig. 1　Distribution of Hybodontoidea in China and scheme map showing fossil locality of Zuodeng, Tiandong County of Guangxi Province, China

1) Yongdeng; 2) Kunming; 3) Lufeng; 4) Guangyuan; 5) Yanchang; 6) Ansai; 7) Qiyang; 8) Yaojie; 9) Tiandong

弓鲛超科　Hybodontoidea Zangerl, 1981

弓鲛科　Hybodontidae Owen, 1846

弓鲛属 *Hybodus* **Agassiz, 1837**

作登弓鲛 *Hybodus zuodengensis* **(Yang et al., 1984)**

(图版I,A～D;图3)

1984　**作登厚齿棒牙形石** *Pachycladina zuodengensis* Yang et al., pl. 18, figs. 11 and 18; pl. 19, fig. 17

正型标本　**一枚完整的牙齿。北京大学地质系标本编号**:PU 83018;**野外编号**:**作**5-5。

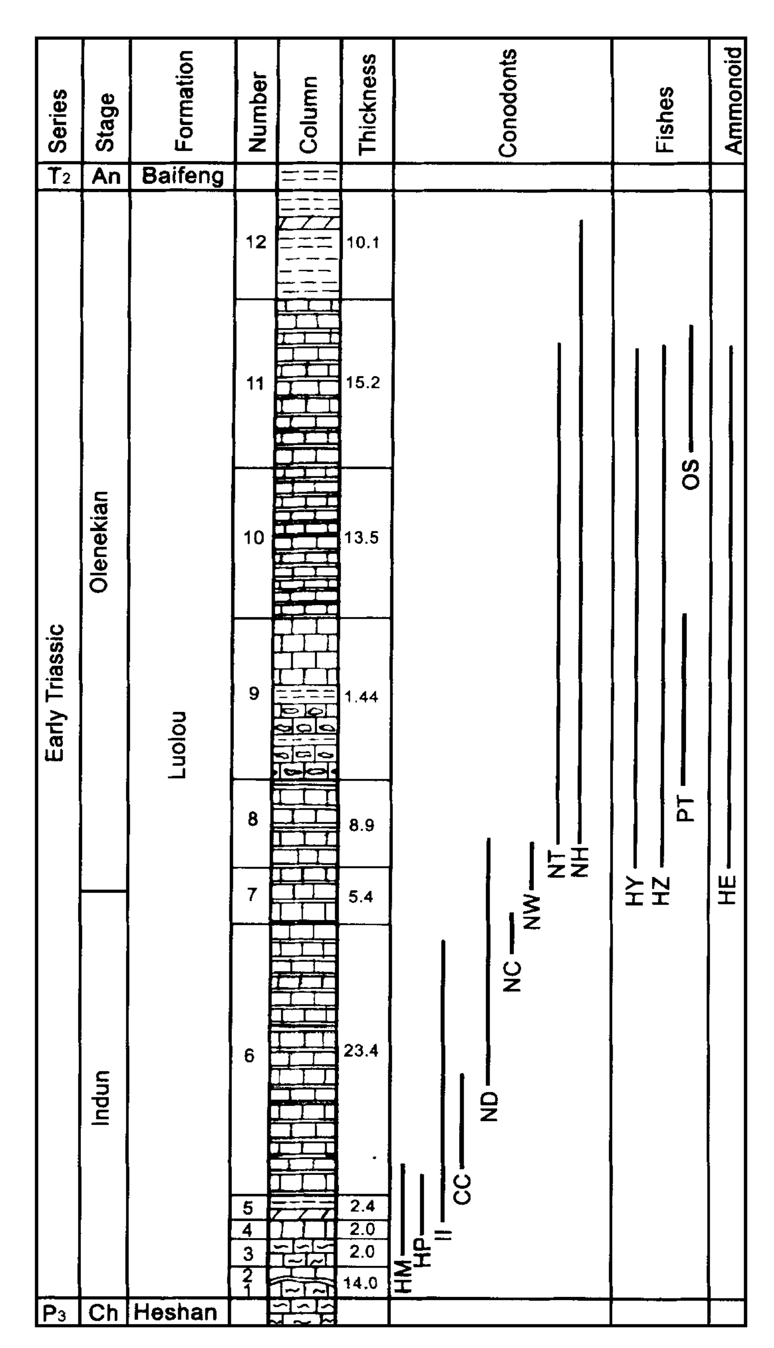


图 2　广西田东县作登下三叠统鱼类、牙形类和部分菊石分布时限
(据杨守仁等 1984 ,略作修改和补充)

Fig. 2　Lower Triassic fishes , conodonts and ammonoid from Zuodeng , Tiandong County of Guangxi Province , China (modified from Yang et al. , 1984)

Fishes : HY *H. yohi* , HZ *Hybodus zuodengensis* , PT *Polyacrodus tiandongensis* and OS Osteichthyes gen. et sp. indet. ; conodonts : HM *Hindeodus minutus* , HP *H. parvus* , II *Isarcicella isarcica* , CC *Clarkina carinata* , ND *Neospathodus dieneri* , NC *N. cristagalli* , NW *N. waageni* , NH *N. homeri* , NT *N. triangularis* ; ammonoid : HE *Hellenites* sp. ; T_2 Middle Triassic , An Anisian , P_3 Late Permian , Ch Changhsingian

标本 3 枚牙齿,其中一枚齿尖略有缺损。中国科学院古脊椎动物与古人类研究所标本编号:IVPP V 12669;野外编号:作 10 - 30。北京大学地质系标本编号:PU 83011 和 PU 83015;野外编号:作 10 - 30 和作 5 - 5。

产地与层位 广西田东县作登;下三叠统罗楼组上部奥伦尼克阶司帕斯早期。

修正特征 牙齿主尖细长,基本位于牙齿中央,向舌面略弯曲。侧尖最多 3 对。主尖和侧尖横截面呈椭圆形。牙齿冠部唇面细脊纹不发育,相反舌面细脊纹略发育,覆盖主尖冠部舌面 2/3 的面积。齿根低,中央略向上弯曲;齿根唇面无小的营养孔,相反舌面和基面却可见很多小的圆形或裂隙状营养孔。

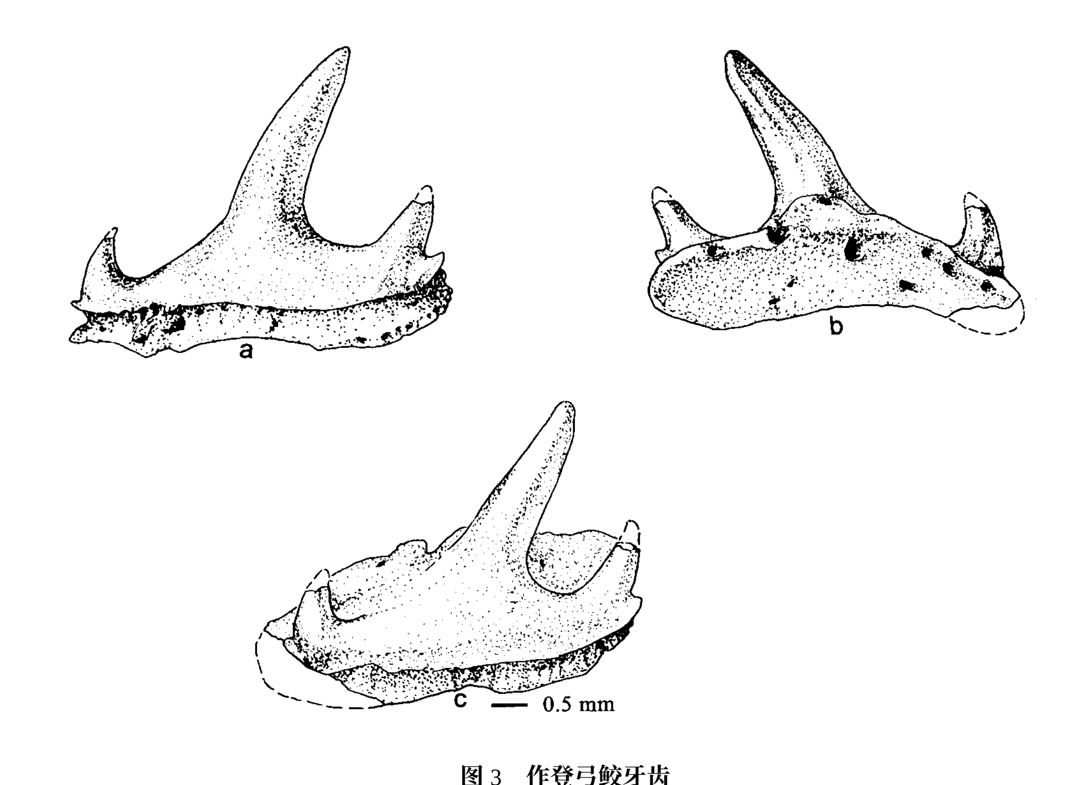


图 3 作登弓鲛牙齿

Fig. 3 Tooth of *Hybodus zuodengensis* (Yang et al., 1984), IVPP V 12669

a) in labial view; b) in lingual view; c) in occlusal view

描述 这里论述的 4 枚牙齿除 PU 83011 号牙齿齿尖略有缺损外,其他 3 枚均为完整牙齿。牙齿由齿冠和齿根构成。齿冠由主尖和侧尖组成。主尖细长,基本位于牙齿中央,向舌面略弯曲。正模标本和 IVPP V 12669 号标本各具 2 对侧尖。PU 83015 具一对侧尖,PU 83011 具 3 对侧尖。主尖和侧尖横截面呈椭圆形。牙齿冠部唇面细脊纹不发育,而舌面细脊纹略发育,向上可达齿尖,但向下不达齿冠基部,细脊纹仅占主尖舌面 2/3 的面积。牙齿在唇面和舌面均不存在辅突。齿根低,中央略向上弯曲,唇面无小营养孔,而舌面却可见小的圆形或裂隙状营养孔,齿根基部也可观察到类似的小孔。冠部长略小于根部长,冠部宽也略小于根部宽。各个牙齿根部的高度相等。

表 1　作登弓鲛牙齿测量

Table 1　Measurements of the teeth of *Hybodus zuodengensis* **(Yang et al., 1984)** (mm)

标本 Specimen	冠部长 Length of crown	冠部宽 Breadth of crown	主尖高 Height of main cusp	根部长 Length of root	根部宽 Breadth of root	根部高 Height of root
PU 83018	1.35	0.2	0.9	1.45	0.3	0.1
IVPP V 12669	1.2	0.3	1.0	1.4	0.6	0.1
PU 83011	1.6	0.25	?	1.6	0.35	0.1
PU 83015	1.0	0.4	1.0	1.2	0.55	0.1

比较　这里叙述的牙齿无疑属于弓鲛属(*Hybodus*)。我国对弓鲛属的化石已有一些报道,包括牙齿和鳍棘(杨钟健,1935,1941,1942;刘宪亭,1962;王念忠,1977;薛祥煦,1980)。与以往记述的弓鲛牙齿最大的区别在于,这里记述的牙齿主尖明显细长,但牙齿冠部的脊纹则不太发育。它与产自斯匹兹贝尔根 Mt. Viking 三叠纪的 *Hybodus sasseniensis* (Stensiö, 1921; Cappeta, 1987)比较相近,比如牙齿主尖细长,侧尖均细小等,但作登的标本明显不同于后者的是,牙齿冠部脊纹不太发育;齿根低,齿根舌面小营养孔发育等。因此,命名作登的标本为作登弓鲛(*Hybodus zuodengensis*)。根据命名法,种名仍沿用其命名为牙形类的种名,该种名表示化石产地。

乐氏弓鲛 *Hybodus yohi* **(Yang et al., 1984)**

(图版 I,E;图 4)

1984　乐氏假舟牙形石 *Pseudogondolella yohi* Yang et al., pl. 18, fig. 8

正型标本　一枚近于完整的牙齿。北京大学地质系标本编号:PU 83008;野外编号:作5 - 5。

产地与层位　广西田东县作登;下三叠统罗楼组上部奥伦尼克阶司帕斯早期。

修正特征　牙齿主尖略高,主尖的一侧具 4 枚侧尖,而另一侧是 3 枚侧尖。主尖和侧尖的横截面大致呈三角形。牙齿冠部细脊纹发育,特别是唇面。冠部唇面下部与牙齿根部间形成一条明显的凹沟。齿根低,不弯曲,唇面和舌面具大小不等的圆形小营养孔,但齿根基面该孔不发育。

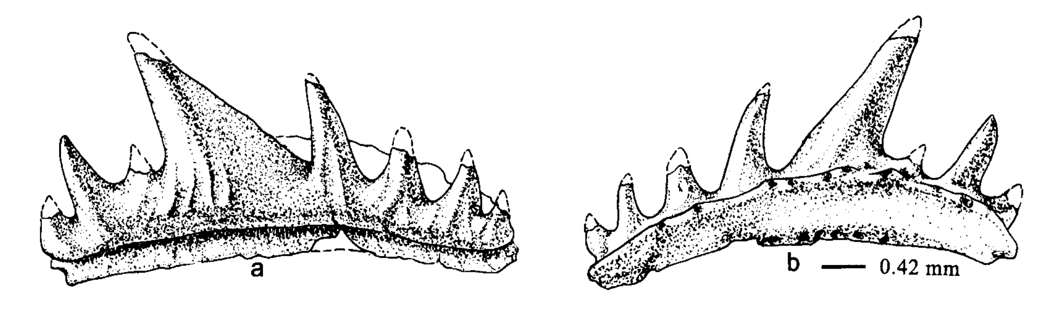


图 4　乐氏弓鲛牙齿

Fig. 4　Tooth of *Hybodus yohi* (Yang et al., 1984), PU 83008

a) in labial view; b) in lingual view

表 2 乐氏弓鲛牙齿测量

Table 2 Measurements of the tooth of *Hybodus yohi* (Yang et al., 1984) (mm)

标本 Specimen	冠部长 Length of crown	冠部宽 Breadth of crown	主尖高 Height of main cusp	根部长 Length of root	根部宽 Breadth of root	根部高 Height of root
PU 83008	1.7	0.4	0.65	1.8	0.6	0.1

描述 一枚近于完整的牙齿,仅个别齿尖略微缺失。牙齿主尖比侧尖略高、粗大,略向舌面弯曲。主尖一侧是 4 枚侧尖,另一侧是 3 枚侧尖,综合主尖两面侧尖形状可以复原牙齿形状。主尖和侧尖横截面大致呈三角形。牙齿的唇面和舌面均无辅突。冠部唇面区分为较大的上部和狭小的下部,两者之间具明显的界线,唇面下部与牙齿根部间形成一条明显的凹沟。牙齿冠部唇面的细脊纹向下可达唇面上、下部分界线处。舌面细脊纹没有唇面的发育。齿根低,不弯曲,唇面和舌面均具大小不等的、圆形小营养孔,但齿根基部该孔不发育。牙齿冠部长略小于根部长,牙齿冠部宽则明显小于根部宽。

比较 这里记述的牙齿在某些方面与产自湖南祁阳中侏罗世的黄泥塘弓鲛(*Hybodus huangnitanensis* Wang, 1977)相似,如牙齿侧尖数目多,牙齿冠部的脊纹发育,牙齿的唇面与根部间有一条明显的凹沟等。但是,它以牙齿尖、齿冠上的脊纹数目少、基部唇面仅具很少的营养孔等特征明显有别于湖南的标本。乐氏弓鲛也不同于作登弓鲛,例如,牙齿的主尖和侧尖的截面大致呈三角形,牙齿冠部细脊纹发育,冠部唇面与牙齿根部间形成一条明显的凹沟等。因此命名其为乐氏弓鲛(*Hybodus yohi*)。根据命名法,种名仍用原来命名为牙形类的名称,种名是为纪念已故的北京大学地质系主任乐森玥先生。

多尖齿鱼科 Polyacrodontidae Glückman, 1964

多尖齿鱼属 *Polyacrodus* Jaekel, 1889

田东多尖齿鱼(新种) *Polyacrodus tiandongensis* sp. nov.

(图版 I, F; 图 5)

正型标本 一枚冠部完整的牙齿。中国科学院古脊椎动物与古人类研究所标本编号:IVPP V 12670;野外编号:作 4 - 28。

产地与层位 广西田东县作登;下三叠统罗楼组上部奥伦尼克阶司帕斯早期。

特征 牙齿厚实,横向扩展,具一大致呈圆锥形、低而钝的主尖。主尖冠部唇面和舌面向外膨胀。唇面和舌面的细脊纹弱。唇面副突略发育。侧尖不发育,牙齿冠部具纵横咬合嵴,但较弱。

词源 田东为化石产地所在的县名。

描述 一枚冠部完整的牙齿,但基部没有保存。牙齿厚实,横向扩展。在牙齿中央具一大致呈圆锥形、低而钝的主尖。主尖冠部唇面和舌面向外膨胀。唇面具短的细脊纹,从主齿尖向下延伸达唇面中部;舌面则具较长的细脊纹,从齿尖向下延伸达冠基部;但唇面和舌面的脊纹均较弱。唇面具唇面副突(labial accessory process),略发育。侧尖不发育。牙齿的两侧缘低。牙齿的纵横咬合嵴(longitudinal and transversal occlusal crests)存在但

细弱;对应的唇面和舌面的横咬合嵴从纵咬合嵴上同一位置发出;唇面横咬合嵴比舌面的横咬合嵴略发育,在齿冠基部形成小结节。

比较　这里记述的牙齿与产自斯匹兹贝尔根 Mt. Congress 三叠纪的 *Polyacrodus angulatus* (Stensiö, 1921) 有某些相似之处,如牙齿只有主尖发育,低而钝;侧尖不发育等。但新标本与斯匹兹贝尔根的标本存在明显的区别,如主尖冠部脊纹弱,相当的侧尖部分低。横咬合嵴弱等。所以,此处叙述的标本被确定为一新种——田东多尖齿鱼(新种) *Polyacrodus tiandongensis* sp. nov.,种名田东(Tiandong)为化石产地所在的县名。就全球范围而言,多尖齿鱼属分布于从下三叠统到上白垩统的地层中,主要见于欧州和格陵兰。

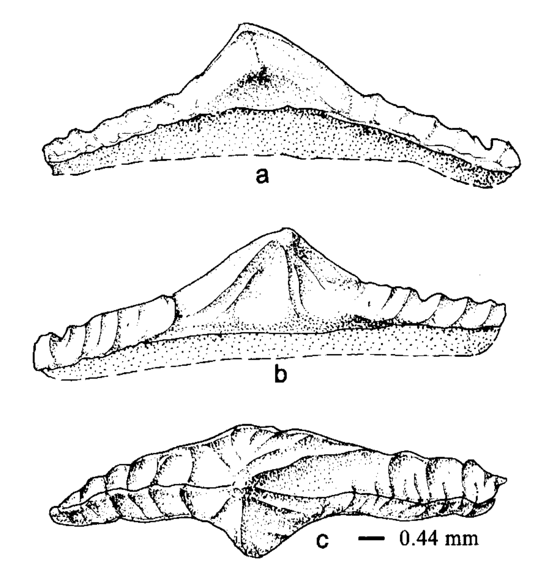


图 5　田东多尖齿鱼(新种)牙齿

Fig. 5　Tooth of *Polyacrodus tiandongensis* sp. nov., holotype IVPP V 12670

a) in labial view; b) in lingual view; c) in occlusal view

表 3　田东多尖齿鱼(新种)牙齿测量

Table 3　Measurements of the tooth of Polyacrodus tiandongensis **sp. nov.**　(mm)

标本 Specimen	冠部长 Length of crown	冠部宽 Breadth of crown	主尖高 Height of main cusp	唇面附突宽 Breadth of labial accessory process
IVPP V 12670	2.4	0.6	0.6	0.2

硬骨鱼纲　**Osteichthyes Huxley, 1880**

硬骨鱼纲(属种未定)　**Osteichthyes gen. et sp. indet.**

(图版 I, G)

标本　一块不完整齿板。中国科学院古脊椎动物与古人类研究所标本编号:IVPP V 12671;野外编号:作 5 - 30。

产地与层位　广西田东县作登;下三叠统罗楼组上部奥伦尼克阶司帕斯早期。

描述　为了全面地了解鱼群的面貌,所以在此将这一不太完整的齿板一并记述。它是一块一端保存自然状态,另一端断裂的齿板,共保存牙齿和齿穴 17 个。从齿板保存部分的形状,特别是单个牙齿的形状看,它无疑属于硬骨鱼类,但难以进一步鉴定。

2　讨论

2.1　田东弓鲛鱼类的重要性

在板鳃鱼类的进化中,可以明显地区分出三个水平:裂齿鲨类水平(cladoselachids,

cladodontids, xenacanthids)、弓鲛鱼类水平(ctenacanthoids, hybodontoids)和现代板鳃鱼类水平(Patterson, 1966; Johnson, 1981; Cappeta, 1987; Goto, 1994; Rieppel et al., 1996)。栉棘鲨类(ctenacanthoids)和弓鲛鱼类(hybodontoids)组成古生代板鳃鱼类的主干,并最终进化出中生代晚期和第三纪的现代鲨类和鳐类。因此,弓鲛鱼类化石的研究对探讨板鳃鱼类的演化具有重要意义。

由于软骨鱼类的骨骼主要由软骨构成,所以在软骨鱼类化石中,除鳞片、鳍棘和牙齿以外的其他部分很少保存为化石。牙齿与鳞片和鳍棘相比,无疑能为我们提供更为重要的信息。此外,牙齿因不与颌骨愈合且彼此依次替换,因而常常可以发现保存很好的单个牙齿。因而,牙齿是软骨鱼类化石研究中最为重要的材料,田东弓鲛鱼类化石即为一例。

田东的材料与以往我国报道的弓鲛鱼类牙齿相比,具有以下特点:以往报道的弓鲛鱼类牙齿化石多为自然状态保存,多半仅仅反映一个牙齿的唇面或舌面形态,甚至牙齿的唇面或舌面的性状也没有完全显示出来,有关牙齿根部的信息则更少(刘宪亭,1962;王念忠,1977;薛祥煦,1980)。田东鱼化石由于是使用弱酸处理含鱼地层的岩样而获得的,所以除个别牙齿齿根没有保存外,绝大多数牙齿能显示牙齿的立体面貌,可以反映牙齿冠部和根部的各种性状。这就为该类化石的正确鉴定和比较提供了良好的条件。

弓鲛属(*Hybodus*)化石以往主要发现于欧洲、北美、西北非和亚洲中三叠世到晚白垩世的沉积中。有关早三叠世化石的报道很少,可能表明二叠纪和三叠纪之交大绝灭后复苏的艰难。田东的弓鲛鱼类化石为研究这次大绝灭后鱼类的复苏提供了重要的材料。

2.2 田东弓鲛鱼类组合带

在我国以往已知的弓鲛鱼类化石中,最早发现的是晚侏罗世的弓鲛鱼类鳍棘(杨钟健,1935),其他化石多见于晚三叠世—中侏罗世地层中(杨钟健,1941,1942;刘宪亭,1962;王念忠,1977;薛祥煦,1980)。田东弓鲛鱼类是我国早三叠世该类鱼的首次报道,也是弓鲛鱼类在我国的最早记录。

特别需要指出的是,由于田东弓鲛鱼类化石与牙形类 *Neospathodus homeri*-*N. triangularis* 带化石一起产出,因此鱼化石的时代可以确定为早三叠世奥伦尼克阶司帕斯期早期。

田东作登登高岭剖面产出的软骨鱼类化石从第8层向上延伸至第11层。分布于8层至11层的牙形类包括 *Cypridodella conflex*, *Hibbardella triassica*, *Prioniodella ctenoides*, *Neospathodus homeri* 和 *N. triangularis*。这正是牙形类 *Neospathodus homeri*-*N. triangularis* 组合带的分布范围。*N. homeri* 和 *N. triangularis* 都是世界性的种,常常一起出现在司帕斯期早期。该牙形类带化石在我国分布广泛,如黔桂罗楼组上段,广西龙丈组,西藏查曲浦群,色容寺组,兰成曲群下组等(杨守仁等,1999)。由于鱼化石和牙形类这一组合带分布时限一致,所以在此建立作登弓鲛—乐氏弓鲛(*Hybodus zuodengensis*-*H. yohi*)鱼化石组合带。此带除上述两类鱼化石外,还包括田东多尖齿鱼(*Polyacrodus tiandongensis*)和一类硬骨鱼类。这是我国三叠纪第一个鱼类化石带,该鱼化石带的特点是以弓鲛超科的化石为主导。作登弓鲛—乐氏弓鲛鱼化石组合带的确立使作登弓鲛鱼类化石具有生物地层学意义,有利于含类似弓鲛鱼类化石的地层对比。

2.3　田东以及我国其他地区弓鲛鱼类的生境

弓鲛鱼类化石在世界各地一般多见于海相地层中,但我国以往的化石均发现于陆相沉积中(杨钟健 1935,1941,1942;刘宪亭,1962;王念忠,1977;薛祥照,1980)。直到王念忠(1977)研究湖南祁阳中侏罗世黄泥塘弓鲛(*Hybodus huangnidanensis*)时,根据鱼群的组成和伴生的其他脊椎动物化石和无脊椎动物化石,认为黄泥塘弓鲛产自河口相沉积中。薛祥煦(1980)根据我国三叠系和侏罗系含弓鲛鱼类化石和相邻地层海陆分布的新资料,认为以往我国发现的弓鲛鱼类化石所生存过的水体可能与海(或与海有关的水体)相沟通。但是,含弓鲛鱼类化石上下地层的资料还难以直接说明上述弓鲛鱼类一定属于海相化石。因此,田东弓鲛鱼类化石成为我国海相弓鲛鱼类化石的首次确切报道。它无疑生活于开放海环境,这可以由与鱼化石一起产出的牙形类和菊石等典型的海相化石证实。我国海相弓鲛鱼类化石的报道为我们进行该类化石的洲际对比和开展海相—非海相对比创造了有利的条件。

表 4　中国弓鲛超科化石记录

Table 4　Fossil records of Hybodontoidea in China

属种 Species	地点 Locality	时代 Age	沉积相 Facies
弓鲛未定种 *Hybodus* sp.	甘肃永登 Yongdeng, Gansu	J_3 or K_1	陆相 Continental
后甸弓鲛 *H. houtianensis* Young, 1941	云南昆明 Kunming, Yunnan	T_3 or J_1	陆相 Continental
弓鲛未定种 *Hybodus* sp.	云南禄丰 Lufeng, Yunnan	T_3	陆相 Continental
弓鲛未定种 *Hybodus* sp.	四川广元 Guangyuan, Sichuan	J_3	陆相 Continental
杨氏弓鲛 *H. youngi* Liu, 1962	陕西延长 Yenchang, Shaanxi	T_3	陆相 Continental
安定弓鲛 *H. antingensis* Liu, 1962	陕西安塞 Ansai, Shaanxi	J_2^3	陆相 Continental
黄泥塘弓鲛 *H. huangnidanensis* Wang, 1977	湖南祁阳 Qiyang, Hunan	J_2	河口相 Estuary
锤纹弓鲛 *H. clavus* Xue, 1980	甘肃窑街 Yaojie, Gansu	J_2	内陆湖盆 Inland lake
双粗纹无尖齿鱼 *Acrodus biserasseplicatus* Xue, 1980	甘肃窑街 Yaojie, Gansu	J_2	内陆湖盆 Inland lake
作登弓鲛 *H. zuodengensis* (Yang et al., 1984)	广西田东 Tiandong, Guangxi	T_1	海相 Marine
乐氏弓鲛 *H. yohi* (Yang et al., 1984)	广西田东 Tiandong, Guangxi	T_1	海相 Marine
田东多尖齿鱼 *Polyacrodus tiandongensis* sp. nov.	广西田东 Tiandong, Guangxi	T_1	海相 Marine

注:T_1 and T_3 Early and Late Triassic; J_1, J_2, J_3 Early, Middle and Late Jurassic; K_1 Early Cretaceous.

2.4　广西罗楼组的鱼类化石

在广西早三叠世罗楼组产出的鱼类,除去田东作登的软骨鱼类和硬骨鱼类外,还有产自凤山抗东的空棘鱼类化石——凤山中华空棘鱼(*Sinocoelacanthus fengshanensis*)(刘宪亭,1964)。

致谢 张文定和杨安国先生摄制电镜照片,侯晋封先生绘制图件。英国自然历史博物馆古生物部 S. Young 女士在第一作者于 2000 年夏季访英期间展示馆藏精美的软骨鱼类标本,其中包括一些完整的弓鲛鱼类化石。作者在此一并致以谢意。

EARLY TRIASSIC HYBODONTOIDEA FROM TIANDONG OF GUANGXI, CHINA

——First Report on the Fish Sequence Study Near the Permian-Triassic Boundary in South China

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Key words Guangxi, marine facies, Early Triassic, Hybodontoidea, fish zonation

Summary

The materials dealt with in this paper were collected from the Luolou Formation of Zuodeng area, Tiandong County of Guangxi Zhuang Autonomous Region, China (Figs. 1,2). They include three hybodontoid species: *Hybodus zuodengensis* (Yang et al., 1984), *H. yohi* (Yang et al., 1984) and *Polyacrodus tiandongensis* sp. nov., and an indeterminate osteichthyan fish. The two species of *Hybodus* were initially identified as conodonts — *Pachycladina zuodengensis* and *Pseudogondalella yohi* by Yang et al. in 1984.

This is the first report on the occurrence of marine Early Triassic Hybodontoidea in China. With the reassignment and new discovery of these fishes, a fish assemblage (*Hybodus zuodengensis*-*H. yohi* Zone) is established, which is the only Triassic fish zonation in China. The age of this zonation is Early Triassic (early Spathian of Olenekian Stage) for it makes its appearance just in the conodont *Neospathodus homeri*-*N. triangularis* Zone.

1 Brief Description of Fish-Bearing Denggaoling Section

The Denggaoling section in Zuodeng area, Tiandong County is an important Lower Triassic section in China. It includes the Lower Triassic Luolou Formation completely and contacts conformably with both the underlying Upper Permian and the overlying Middle Triassic strata. This section can be subdivided into 8 conodont zones in ascending order: *Hindeodus minutus* Zone, *H. parvus* Zone, *Isarcicella isarcica* Zone, *Clarkina carinata* Zone, *Neospathodus dieneri* Zone, *N. cristagalli* Zone, *N. waageni* Zone, and *N. homeri*-*N. triangularis* Zone. The hybodontoid fossils described in this paper occur in the *Neospathodus homeri*-*N. triangularis* Zone, from eighth to eleventh beds of the section (Fig. 2).

Overlying strata: Middle Triassic Baifeng Formation

——Conformity——

Lower Triassic Luolou Formation 98.35m

12. Grey calcareous mudstone intercalated with marl yielding conodonts: *Neospathodus* cf. *homeri* and others 10.1m

11. Dark gray medium to thick bedded limestone with mudstone zebra yielding conodonts: *Neospathodus homeri*, *N. triangularis* and others; ammonoid: *Hellenites* cf. *pracmaturus*; and fishes: *Hybodus zuodengensis*, *H. yohi* and Osteichthyes gen. et. sp. indet.	15.2m
10. Grey to dark gray thin bedded limestone with mudstone zebra, yielding conodonts: *Neospathodus* spp. and others	13.5m
9. Light red to gray thin-bedded lenticular limestone intercalated with mudstoneshale yielding conodonts: *Neospathodus homeri*, *N. triangularis*; and fish: *Polyacrodus tiandongensis*	1.44m
8. Mudstoneshale intercalated with gray thin bedded limestone with mudstone zebra yielding conodonts: *Neospathodus homeri*, *N. triangularis*, *N.* cf. *dieneri*; fishes: *Hybodus zuodengensis*, *H. yohi*; and ammonoid: *Hellenites* sp. at the bottom	8.9m
7. Grey thin-bedded limestone with mudstone zebra, yielding conodonts: *Neospathodus cristagalli*, *N. waageni*; and ammonoid: *Hellenites* sp.	5.4m
6. Grey thin-bedded limestone with mudstone zebra intercalated with mudstoneshale yielding conodonts: *Neospathodus cristagalli*, *N. dieneri*, *Isarcicella isarcica*, *Hindeodus parvus*, *H. minutus*	23.4m
5. Cream-colored mudstone to gray marl yielding conodont fragments in the lower part	2.4m
4. Grey thick-bedded bioclast limestone yielding conodonts: *Hindeodus parvus*, *Isarcicella isarcica*, and rich gastropods and ostracods	2.0m
3. Dark gray thick-bedded spotted limestone yielding conodonts: *Hindeodus minutus*	2.0m
2. Grey thick-bedded limestone intercalated with bioclast limestone yielding conodont: *Hindeodus* sp., and rich gastropods and ostracods	4.1m
1. Dark gray thick-bedded spotted limestone intercalated with gray thick-bedded limestone and with pyrite crystal in the limestone, yielding ostracods	9.9m

——Conformity——

Underlying strata: Upper Permian Heshan Formation

2 Systematics

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Superfamily Hybodontoidea Zangerl, 1981

Family Hybodontidae Owen, 1846

Genus *Hybodus* **Agassiz, 1837**

Hybodus zuodengensis **(Yang et al., 1984)**

(Pl. I, A～D; Fig. 3)

1984 *Pachycladina zuodengensis* Yang et al., pl. 18, figs. 11 and 18; pl. 19, fig. 17

Holotype A complete tooth. Catalog number of the Peking University: PU 83018; field number: Zuo 5 - 5.

Material Three complete or nearly complete teeth. Catalog number of the Institute of Vertebrate Paleontology and Paleoanthropology: IVPP V 12669; field number: Zuo 10 - 30. Catalog numbers of the Peking University: PU 83011 and PU 83015; field numbers: Zuo 10 - 30 and Zuo 5 - 5.

Locality and horizon Zuodeng district, Tiandong County of Guangxi Zhuang Autonomous Region. Lower Triassic Luolou Formation (early Spathian of Olenekian Stage).

Emended diagnosis Dentition heterodont, central cusp high, slender and arched lingually; maximum three pairs of lateral cusps; cross section of the central and lateral cusps elliptical; labial face of crown with undeveloped striae but lingual face of the crown with weakly developed striae and covering two-thirds of central cusp; root low with weakly bent centre

and upwards; labial face of the root without any nutrient foramen but lingual and basal faces of the root with numerous small and rounded or creviced nutrient foramina.

Etymology Zuodeng, fossil locality.

Remarks *Hybodus zuodengensis* (Yang et al.) differs from *H. youngi* Liu, 1962 and *H. antingensis* Liu, 1962 (from the Late Triassic and Middle Jurassic in Shaanxi), *H. huangnidanensis* Wang, 1977 (from the Middle Jurassic of Hunan), and *H. clavus* Xue, 1980 (from the Middle Jurassic of Gansu) in having a higher and slender central tooth cusp and in without developed tooth crown striae. It resembles *H. sasseniensis* Stensiö, 1921 (from Triassic of Spitsbergen) in some aspects such as a high and slender central cusp, small lateral cusps, but it is different from the latter in without developed tooth crown triae, lower tooth root and lingual face of the root with developed small nutrient foramina.

Hybodus yohi **(Yang et al., 1984)**
(Pl. I, E; Fig. 4)

1984 *Pseudogondolella yohi* Yang et al., pl. 18, fig. 8

Holotype A nearly complete tooth. Catalog number of the Peking University: PU 83008; field number: Zuo 5-5.

Locality and horizon As for *Hybodus zuodengensis* (Yang et al., 1984).

Emended diagnosis Dentition heterodont, central cusp slightly high, four cusps in one side of the central cusp and three in another one, cross section of central and lateral cusps roughly triangular; tooth crown with developed triae, particularly in labial face of the crown; a groove between the labial face of tooth crown and root; root low, labial and lingual faces with small rounded nutrient foramina.

Etymology Yoh, family name of the late Professor S. S. Yoh of the Peking University.

Remarks The tooth described here resembles *Hybodus huangnidanensis* (Wang, 1977) in some aspects, such as tooth consisting of a number of secondary cusps, developed striae in both principal and secondary cusps, and a clear groove between the tooth crown and root. But it differs from the latter in its tooth having higher and slender cusps, tooth crown with fewer striae, and only a few of nutrient foraminae in labial face of the tooth root. It differs from *Hybodus zuodengensis* in the cross section of central and lateral cusps being triangular, the crown with developed triae and a clear groove between the tooth crown and root.

Family Polyacrodontidae Glückman, 1964

Genus *Polyacrodus* **Jaekel, 1889**

Polyacrodus tiandongensis, **sp. nov.**
(Pl. I, F; Fig. 5)

Holotype A tooth with complete crown. Catalog number of the Institute of Vertebrate Paleontology and Paleoanthropology: IVPP V 12670; field number: Zuo 4-28.

Locality and horizon As for *Hybodus zuodengensis* and *H. yohi*.

Diagnosis Tooth massive and expanded transversely, principal cusp more or less pyramidal, low and blunt and expanded in both labial and lingual sides of the principal cusp, the labial face of the principal cusp with a labial accessory process, both the labial and lingual faces of the principal cusp with light crests. Secondary cusps undeveloped, the principal cusp and its two lateral sides carrying a longitudinal occlusal crests and the latter with numerous transverse occlusal crests, but both crests light.

Etymology Tiandong, county of the fossil locality.

Remarks The tooth described here resembles that of Triassic *Polyacrodus angulatus* (Stensiö, 1921) from Mt. Congress of Spitsbergen in the presence of low and blunt principal

cusp and in the absence of secondary cusps. But it differs from the latter in its light labial, lingual and occlusal crests on the principal cusp, and low lateral sides of the principal cusp.

Osteichthyes gen. et sp. indet

(Pl. I, G)

Material An incomplete tooth plate, IVPP V 12671, field number: Zuo 5 - 30.

Locality and horizon As for the hybodontoids.

Description This is an incomplete tooth plate with seventeen teeth or tooth sockets. It should be an osteichthyan fossil according to its tooth morphology, but further identification for the fossil can not be made based on the present specimen.

3 Discussions

3.1 Materials of Hybodontoidea of Tiandong County

Compared with hybodontoid teeth described before in China, the materials of Tiandong are stereoscopic teeth, and they are most informative with the complete characters of labial, lingual and occlusal faces of the tooth crown and those of labial, lingual and basal faces of the tooth root, except for character of root of species *Polyacrodus tiandongensis*.

Hybodus is mainly discovered from the Middle Triassic to Late Cretaceous strata in Europe, North America, North and West Africa, and Asia. Rare reports for the Early Triassic fishes indicate that biotic recovery is very difficult after the Permian/ Triassic extinction.

3.2 Zonation of Hybodontoidea in Tiandong County

We erected a new fish zonation *Hybodus zuodengensis*-*H. yohi* assemblage zone (AZ), which is composed of *Hybodus zuodengensis* (Yang et al.), *H. yohi* (Yang et al.), *Polyacrodus tiandongensis* sp. nov., and Osteichthyes gen. et sp. indet. It ranges from the eighth to eleventh layers in the Denggaoling section of Zuodeng area (Fig. 2), and its age is Early Triassic (early Spathian of Olenekian Stage) after the contemporary conodont *Neospathodus homeri*-*N. triangularis* Zone.

3.3 Habitat of Hybodontoidea in China

The fossil fishes of Tiandong lived in an open sea environment according to the associated conodont and ammonoid fossils and the data of depositional facies. This is the first report on the occurrence of marine Early Triassic hybodontoids in China, because the other known hybodontoid fossils were recovered from the continental facies of Late Triassic to Late jurassic (or to Early Cretaceous) in Gansu, Yunnan, Sichuan, and Shaanxi provinces (Young, 1935, 1941, 1942, fin spines; Liu, 1962, teeth; Xue, 1980, teeth) and from the estuary facies of Middle Jurassic of Hunan Province (Wang, 1977, teeth) (see Table 4).

3.4 Fishes from the Luolou Formation of Guangxi

There are three classes of fishes discovered from the Luolou Formation in Guangxi Zhuang Autonomous Region:

Chondrichthyes (from Tiandong County)
- *Hybodus zuodengensis* (Yang et al., 1984)
- *Hybodus yohi* (Yang et al., 1984)
- *Polyacrodus tiandongensis* sp. nov.

Osteichthyes gen. et sp. indet. (from Tiandong County)

Sarcopterygii. Actinistia (from Fengshan County)
- *Sinocoelacanthus fengshanensis* Liu, 1964

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图版 I 说明 (Explanations of Plate I)

A～D. **作登弓鲛** *Hybodus zuodengensis* (Yang et al., 1984)

A. IVPP V 12669; B. PU 83011; C. PU 83015; D. **正型标本**(Holotype), PU 83018; Aa. Ba. Ca. Da. **唇面视**(in labial view); Ab. Bb. Cb. Db. **舌面视**(in lingual view); Ac. Cc. Dc. **咬合面视**(in occlusal view)

E. **乐氏弓鲛** *Hybodus yohi* (Yang et al., 1984)

正型标本(Holotype), PU 83008, Ea. **唇面视**(in labial view); Eb. **舌面视**(in lingual view)

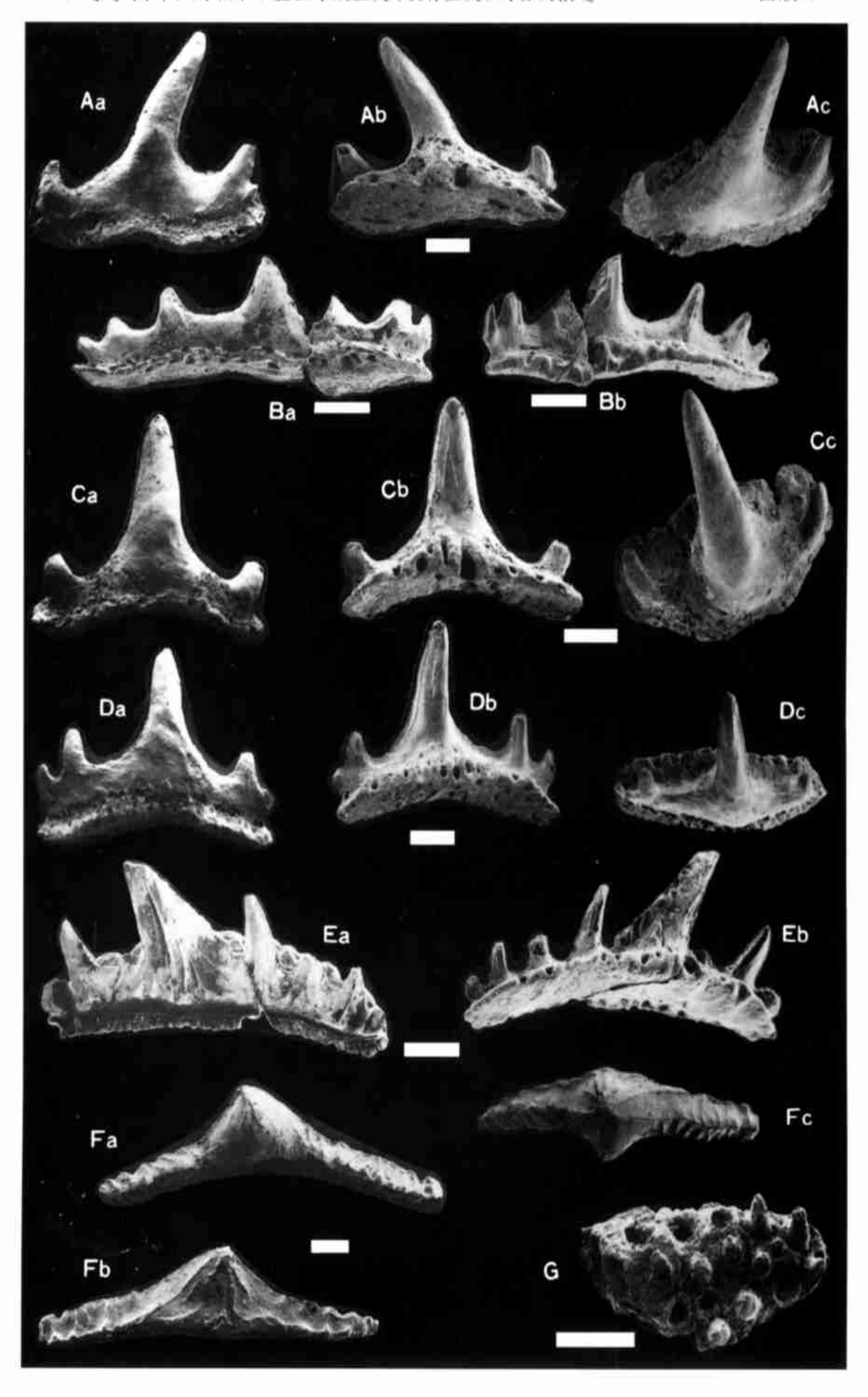
F. **田东多尖齿鱼(新种)** *Polyacrodus tiandongensis* sp. nov.

正型标本(Holotype), IVPP V 12670, Fa. **唇面视**(in labial view); Fb. **舌面视**(in lingual view); Fc. **咬合面视**(in occlusal view)

G. **硬骨鱼纲未定属种**(Osteichthyes gen. et sp. indet.)

齿板(tooth plate), IVPP V 12671

比例尺为 0.25mm (scale bar = 0.25mm)


Aa
Ab
Ac
Ba
Bb
Ca
Cb
Cc
Da
Db
Dc
Ea
Eb
Fa
Fc
Fb
G